

LOWER PALAEOZOIC GREEN ALGAE FROM  
SOUTHERN SCOTLAND, AND THEIR  
EVOLUTIONARY SIGNIFICANCE



BY

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# LOWER PALAEOZOIC GREEN ALGAE FROM SOUTHERN SCOTLAND, AND THEIR EVOLUTIONARY SIGNIFICANCE

By G. F. ELLIOTT

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## ABSTRACT

Ordovician and Silurian green algae (Chlorophyta) from the Girvan area, southern Scotland are described. Species are described, recorded and discussed of the genera *Dimorphosiphon* (Codiaceae); *Vermiporella*, *Intermurella* gen. nov., *Dasycorella*, *Novantiella* gen. nov., *Mastopora* (Dasycladaceae); and *Ischadites* (Receptaculitaceae). The differences between *Dimorphosiphon* and the similar Recent genus *Halimeda* are discussed. The alleged reproductive structures of *Mastopora parva* are considered inorganic in origin. An early non-calcified growth-stage of *M. fava* is described. *Ischadites* is compared with the living non-calcified *Dictyosphaeria*.

The primitive character of this algal flora is related to the main course of Dasycladalean evolution. This is explained in terms of progressive elaboration in ontogeny and phylogeny of the vegetative thallus, against the unaltered reproductive mechanism of large-nucleus fragmentation to give peripheral reproductive bodies, the whole documented for the fossils by very variable calcification as between different genera. The progressive elaboration of Dasycladacean reproductive structures during evolution conferred no apparent advantage on them as compared with other algae.

## INTRODUCTION

ALTHOUGH the Ordovician of the Girvan area of Southern Scotland is well-known for the ubiquitous blue-green alga *Girvanella* and the red alga *Solenopora*, little attention has been paid to the interesting green algae which occur there. Currie & Edwards (1943) described species of Girvan *Mastopora* (Dasycladaceae) in some detail, and it was a re-examination of this material in the Mrs Robert Gray collection, and also other specimens from a part of the Garwood Collection, both housed in the British Museum (Natural History), that led to the present study. This has proved unexpectedly rewarding, for although the programme of thin-sectioning did not yield the exact evidence sought for the initial enquiry, it has revealed much else, and has helped towards a fresh evaluation of the evolution of the Dasycladales.

## Part II

## SYSTEMATIC DESCRIPTIONS

## Class CHLOROPHYCACEAE

## Order SIPHONALES Blackman &amp; Tansley, 1902

## Family CODIACEAE Kützing orth. mut. Hauck, 1884

## Genus DIMORPHOSIPHON Høeg 1927

*Dimorphosiphon rectangulare* Høeg

Pl. 1; Pl. 2, figs 4, 5.

REMARKS. This very characteristic species, familiar from the Norwegian Ordovician, is now recognized from Scotland. It occurs in the type Craighead Limestone, Caradocian, Upper Ordovician, and in the collections studied is represented by random thin-sections of segments (Pl. 2, figs 4, 5). These show the very coarse medullary threads and the thinner lateral or cortical threads. Segment diameters vary from 2.21–2.6 mm, with an incomplete segment length of 6.24 mm seen. The diameters of the central threads are about 0.234 mm, and those of the lateral threads 0.052–0.065 mm. About 21 central threads are seen in one example. These examples compare well with the Norwegian type-material, where segments have a length of 10 mm, and diameter of 2.5 mm, central threads show a diameter of 0.2–0.3 mm, and lateral threads 0.08–0.12 mm, with from 7 to 25 central threads seen in different transverse sections.

DISCUSSION. The striking resemblance between the Ordovician *Dimorphosiphon* and the later *Halimeda* (Cretaceous–Recent) was discussed by Høeg in his original description (Høeg, 1927) and has been noted by all subsequent workers (e.g. Johnson 1961). The long straight coarse medullary threads and divergent finer lateral threads of the Ordovician genus are surprisingly reminiscent of those of the more familiar and widely-distributed *Halimeda*.

However, there are important points of difference.

1. In *Dimorphosiphon* the cortical (lateral) branches are fewer, straighter and only occasionally achieve the characteristic repeatedly swollen terminal divisions of *Halimeda*, and these are never crowded as in *Halimeda*.
2. The internodes (connecting threads between calcified segments), are not known for *Dimorphosiphon*, but although some communication or division of main threads must have occurred (since different segments often have different numbers of threads), yet the several complex internode patterns described for living *Halimeda* (Hillis 1959) are very unlikely to have been present in *Dimorphosiphon*. This latter seems to have been generally more simple in structure.
3. So far as is known, *Dimorphosiphon* did not show the great variety of segment-shape (cf. Hillis 1959) of *Halimeda*.

*Dimorphosiphon* thus appears to represent an early achievement of one of several of the thread- and growth-patterns seen in segmented codiaceans, which I have listed elsewhere (Elliott 1970a, Key p. 331). When this particular pattern reappears later in *Halimeda*, possibly as a result of hybridization in the Cretaceous between the Mesozoic *Boueina* and *Arabicodium* stocks (Elliott 1965) it is much more elaborate, and from Upper Cretaceous onwards *Halimeda* has replaced the other calcified segmented codiaceans in a vigorous evolutionary diversification through Tertiary to Recent. It thus represents a later much more successful varied and elaborate achievement of the thread- and growth-pattern seen in *Dimorphosiphon*. Unlike the latter, which became extinct, *Halimeda* has replaced not merely other calcified codiaceans in the appropriate marine ecologies but in great part dasycladaceans as well, (Elliott 1968, 100–101).

## Order DASYCLADALES Pascher 1931

Family DASYCLADACEAE Kützing orth. mut. Hauck, 1884

Tribe DASYPORELLEAE Pia, 1920

Genus *Vermiporella* Stolley 1893

DIAGNOSIS (after Stolley emend. Pia). Branching curved calcareous tubes with variable wall-thickness and proportionally large stem-cell cavity ( $d/D$  ratio 60% or more). Evidence of primary branches only, the pores usually widening outwards in diameter, and set at or near right-angles to the stem-cell. The pores are irregularly close-set, and not arranged in verticils. Palaeozoic, especially Lower Palaeozoic. Type-species *V. fragilis* Stolley.

*Vermiporella eisenacki* sp. nov.

Pl. 3, figs 1, 2.

DIAGNOSIS. *Vermiporella* species with an external tube-diameter of about 0.4–0.5 mm, probably anastomosing like *Vermiporella* sp. of Eisenack (1936). Ordovician of Scotland.

DESCRIPTION. Forked, bent, branching and probably anastomosing tangled hollow calcareous tubular thallus. External diameter 0.39–0.52 mm, narrowing slightly between points of branching or junctions where it widens. Calcification thin and rather variable, so that the relation of inner to outer diameter of the tubular structures is 60–70%. The branch-pores are set irregularly but closely in the calcification, not in verticils, with the pore-interstices wider than the outer pore-diameters. In section the pores are seen to widen from within outwards; they are rather variable in size but often show an outer diameter of 0.040 mm.

HOLOTYPE. The specimen figured in Pl. 3, fig. 2, from the Stinchar Limestone, Caradocian, Upper Ordovician: Tramitchell Quarry, Girvan, Scotland. British Museum (Natural History), Department of Palaeontology, reg. no. V.54162b.

PARATYPES. The specimen figured in Pl. 3, fig. 1, and one other; same locality and horizon as the holotype. Reg. nos. V.54162a, V.54162b.

REMARKS. *Vermiporella* is an extremely difficult genus for which to allocate species. Specimens allotted to it consist of primitive very simple dasycladacean tubes of protean morphology, perforated by very variable branch-pores, and normally occurring fossil in a fragmentary condition. Stolley's description of the type-species *V. fragilis* (Stolley, 1893) is inadequate by present-day standards, and the holotype is missing. For this reason most workers (e.g. Høeg, 1932; Gnilovskaya, 1965) have classified their material largely on differences in the local florules studied.

*V. eisenacki* is very similar to the *Vermiporella* sp. described by Eisenack (1936). This came from a silicified Silurian Baltic erratic, and was isolated three-dimensionally by acid treatment, the thallus being seen as tangles of bent, branched, anastomosing tubes, of about 0.45–0.60 mm diameter. *V. eisenacki* differs in showing clear pore-structure, a smaller tube diameter, and in being accurately localized in the

Ordovician. Both these species differ from *V. affluens*, *V. acerosa*, and *V. wesenbergensis* (all of Gnilovskaya, 1965), from *V. borealis*, *V. inconstans*, and *V. sp.* (all of Høeg, 1932), and from *V. canadensis* Horne & Johnson (1970).

*Vermiporella* cf. *borealis* Høeg

Pl. 5, fig. 1.

REMARKS. Høeg (1932) described this Norwegian species and records 'abundant, but rather poorly preserved fragments' of this species in the type Craighead Limestone, Caradocian, Upper Ordovician. In the Scottish thin-sections now studied, rather variable vermiporellid fragments are common. These are presumably the same as those on which Høeg based his identification, and one is now figured as *V. cf. borealis*.

*Vermiporella* sp.

Pl. 5, fig. 3.

REMARKS. A large very thin-walled *Vermiporella* sp. occurs uncommonly in the Stinchar Limestone (Caradocian, Upper Ordovician), of Benan Burn, Barr, Ayrshire. It is quite distinct from the common Stinchar Limestone *V. eisenacki*, but the material available is insufficient for description.

Genus *INTERMURELLA* gen. nov.

DIAGNOSIS. Large vermiporellid dasycladacean (external diameter of nearly 2 mm) differing from *Vermiporella* in being straight, slightly curved or slightly sinuous, and not branching, forking or anastomosing. Ordovician of Scotland.

TYPE-SPECIES. *I. scotica* sp. nov.

*Intermurella scotica* sp. nov.

Pl. 3, fig. 1; Pl. 4.

DIAGNOSIS. *Intermurella* of about 2 mm external diameter, d/D ratio 55–60%; the close-set non-verticillate pores are irregularly funnel-shaped, widening outwards.

DESCRIPTION. Irregularly-sinuous elongate-claviform hollow calcareous dasycladacean tube, circular in cross-section, length of 8.06 mm, (holotype) with external diameter of 1.90 mm, internal diameter of 1.04 mm, d/D 55–60%. Smaller examples occur; also a larger example of 10.92 mm length (incomplete). The pores are irregularly close-set, and not in verticils. In section the pores are variable irregular funnel-shaped, with narrow insertions to the stem-cell cavity and widening suddenly to cup-shaped at about halfway in the wall-thickness, so that inside the pore-interstices are wider than the pores and outside the pores wider than the interstices. Inner pore-diameters are 0.026–0.040 mm, maximum pore-diameters, at or just below the outer surface, are about 0.090 mm. About 40 pores are seen in an average transverse section.

**HOLOTYPE.** The specimen figured in Pl. 4, fig. 1, from the Craighead Limestone, Caradocian, Upper Ordovician: Craighead, nr. Girvan, Ayrshire, Scotland. Reg. no. V.55302a.

**PARATYPES.** The specimens figured in pl. 4, figs 2, 3; same locality and horizon, reg. nos. V.55302b, c.

**REMARKS.** *Intermurella*, though primitive in structure, is a distinctive new genus. The name refers to the type-area, in southern Scotland, this being situated in the country between the Roman Hadrianic and Antonine Walls.

Genus **DASYPORELLA** Stolley 1893

*Dasy porella* cf. *norvegica* Høeg

Pl. 2, figs 1, 2.

**DESCRIPTION.** Thick-walled bluntly-claviform, almost cylindrical, hollow calcareous tube with closed rounded termination, circular in cross-section. The largest example showed an external diameter of 1.56 mm, and internal diameter of 0.52 mm, giving a d/D ratio of 33%. In transverse cut about 70 near-straight closely-packed radial branches are seen: branch-diameter is about 0.020 mm. An example with length of 2.03 mm, showed external diameter of 0.91 mm, internal diameter 0.39 mm, with d/D ratio of 43%.

**REMARKS.** This species is very similar to the Scandinavian *D. norvegica* Høeg, which differs only in larger size (external diameter 2.25–4.00 mm). The Scottish fossils may be merely small examples of the Norwegian species. They occur in the type Craighead Limestone, Caradocian, Upper Ordovician.

Høeg (1961) discussed Californian Silurian algae referred by Johnson & Konishi (1959) to *Dasy porella*, but showing a different, non-dasycladacean, branch-structure to *D. norvegica* which is less well-preserved. Stolley's type-specimen of the type-species *D. silurica* is missing. In spite of the uncertainties discussed in full by Høeg, it seems best to conclude with him that probably the Californian algae belong to a different genus to *D. norvegica*, and the Scottish specimens now described are compared with the species *D. norvegica* as conventionally understood.

Genus **NOVANTIELLA** gen. nov.

**DIAGNOSIS.** Cylindrical calcareous dasycladacean tube with wide central cavity and non-verticillate close-pressed swollen primary side-branch cavities separated only by very thin calcification. Ordovician of Scotland. Type-species *Novantiella ordoviciana* sp. nov.

*Novantiella ordoviciana* sp. nov.

Pl. 6.

**DIAGNOSIS.** *Novantiella* of 10 mm length or more, external diameter up to 2.26 mm, d/D ratio 53–63%; diameters of primary branch-cavities are 10 or 11 times or more the thickness of the thin separating calcification.



**DESCRIPTION.** This is a fragile very lightly-calcified dasycladacean tube. A crushed example measures 10.4 mm in length. Transverse sections of uncrushed examples show circular cross-section with external diameters ranging from 1.69–2.26 mm. The stem-cell cavity is moderately wide, the relation of internal to external diameter varying from 53–63%. The wall consists essentially of the cavities left by the side-branches with very little intervening calcification. These branch-cavities are very close-packed, irregularly set, cylindrical in form, rounded polygonal in cross-section, with a length (at right-angles to the stem-cell) varying from 0.31–0.44 mm in different sized examples, but approximately consistent in each separate example. Diameters in cross-section range from 0.091–0.117 mm wide; they are a little more variable, due to crowding, than the lengths.

The calcification which outlines these structures is very thin. It consists of straight, near-parallel calcareous walls of 0.010 mm or often less thickness between branches, terminating outwards at the curved plane of the cylindrical thallus without any elaboration whatsoever. At the inner, stem-cell cavity termination they are very slightly clubbed (to twice wall-thickness or less); this is interpreted as a very slight development of the usual initial constriction of side-branches coming off a dasycladacean stem-cell.

**HOLOTYPE.** The specimen figured in pl. 6, fig. 1, from the Lower Ardmillan Series, Balclatchie Group, Caradocian, Upper Ordovician; Balclatchie, Girvan, Ayrshire. Reg. no. V.16124a.

**PARATYPE.** The specimen figured in pl. 6, fig. 2, same locality and horizon, reg. no. V.16124b.

**REMARKS.** *Novantiella* must in life have been a juicy green alga, with swollen stem-cell, and thick crowded side-branches separated only by the lightest of calcification. The living *Dasycladus* itself shows such a light calcification, though situated differently (around the stem-cell). In structure *Novantiella* is no more advanced in general plan than the vermiporellid *Intermurella* previously described, though the proportions are quite different. In both, of course, it is possible that the primary branches may have divided in an outer zone of which no calcified evidence remains.

*N. ordoviciana* also occurs rarely in the type Craighead Limestone (V.55325b).

The name commemorates the old Celtic tribe Novantae in southern Scotland in Roman times.

#### Tribe **CYCLOCRINEAE** Pia, 1920

#### Genus **MASTOPORA** Eichwald 1840

**REMARKS.** *Mastopora*, long regarded as a problematic genus and variously allocated, was referred to the Dasycladaceae by Stolley (1896) and Pia (1927). It is an early manifestation of one of the several distinctive morphological patterns found recurrently in the Dasycladaceae, and still to be seen in the living *Bornetella*. In this pattern the side-branches radiate from the central stem-cell, and divide into smaller branches, which form expanded cup- or plate-like adjacent terminations

which calcify lightly and so give a hollow thallus, whether club-shaped or subspherical.

Two species of *Mastopora* have been described from the Girvan Lower Palaeozoic; *M. parva* (Nicholson and Etheridge) Pia, a claviform Ordovician species, and *M. fava* (Salter) Stolley, subspherical and Silurian in age (Pl. 7, fig. 3). These were revised and described in some detail by Currie and Edwards (1943). A very important part of this description was the internal structure of *M. parva*, said to show sporangia or reproductive structures on the branches, subsurface to the outer cortex. This was most important, for Pia (1920), in dealing with dasyclad evolution as a whole, had postulated that such a position for reproductive structures (choristospore stage) had not evolved until the later Mesozoic. No detailed internal structure could be described for *M. fava*, by reason of the state of preservation of the material.

A revision of these two species, particularly of internal structure, was therefore undertaken by me. Preparation of new thin-sections failed to furnish new evidence for *M. parva*, so a detailed re-examination has been made of the original diagnostic section. On the other hand, important new evidence has been revealed for *M. fava*, which has some indirect bearing on *M. parva*. This is set out below under the species descriptions.

### *Mastopora parva* (Nicholson and Etheridge) Pia

Pl. 5, fig. 2; Pl. 7, figs 1, 2; Pl. 8, figs 1-3.

DESCRIPTION. (a) *External* (abridged from Currie and Edwards). Alga club-shaped or nearly cylindrical with a tapering base and a rounded apex. A large complete specimen is 54 mm long and 10 mm wide at the broadest point; smaller individuals occur. The diameter of the hexagonal cups varies from 0.6-0.7 mm though the surface is usually too worn for accurate measurement. In surface view the small central pore which is the tubular end of the lateral branch is occasionally to be seen.

(b) *Internal*. This is based on the same thin-section figured by Currie and Edwards (1943): their text-fig. p. 236, and their plate 11, figs 8, 9. It is now re-described.

This transverse section is of a very slightly compressed individual, the outer diameter being a little over 10 mm. The central stem-cell cavity is circular and matrix-filled and is about 2.5 mm diameter, 25% or a little less of the outer diameter. From it there radiate conspicuous spoke-like primary branches. These are incompletely preserved, some origins, mid-portions and terminations being variously seen and all incomplete in a matrix of sparry and other calcite. At one point there are indications of secondary branching. This was probably general, for though it is impossible to count the exact number of primary branches at the stem-cell cavity and the number of outer hexagonal cups in which branches terminate, the number of cups is obviously much in excess of primaries, and secondary branches would be necessary to accommodate this as in other genera with similar morphology.

The outer hexagonal cups show in this section as funnel- or cup-shaped, open outwards and mostly matrix-filled (one contains a possible calcite-filled ostracod).

Currie and Edwards give maximum cup-dimensions as 1.05 mm depth and 0.75 width.

Currie and Edwards (1943, p. 237) claimed to have discovered sporangia in this slide: their account runs 'Immediately below the cups is a zone containing a more or less continuous ring of roughly circular areas, 0.6 mm in diameter. These are interpreted as sporangia. A few somewhat similar bodies lie near the central tube, but it is not absolutely certain that they are of the same nature as those forming a ring near the periphery. The presumed sporangia contain a dark green mineral associated with calcite. There are also idiomorphic quartz grains in the slide, of approximately the same size as the sporangia'.

A careful re-examination shows that all these bodies are polygonal cross-sections of crystals, sometimes corroded and often replaced by a green mineral. Although many are subperipheral several occur further in the interior, and in one case a longitudinal crystal section is seen in the plane of section. Mr P. M. Game, Department of Mineralogy, British Museum (Natural History), kindly examined them petrographically and reports that they are probably garnets partly replaced by chlorite. I see no reason to consider them as remains of sporangia: moreover, similar crystals occur in another *Mastopora* in an immature, pre-reproductive stage (see under *M. fava*).

Regrettably, I cannot agree to this specimen as a very early example of choristospore reproductive structure.

There are other claims of this kind which have been made for Palaeozoic Dasycladaceae: these are the Ordovician *Mastopora pyriformis* (Bassler) Johnson (Osgood & Fischer, 1960); the Permian *Permopora* (Elias, 1947); *Ischadites* (Kesling & Graham, 1962); and the Carboniferous *Koninckopora* (Wood, 1943).

Osgood & Fischer (1960, p. 899) record a thallus-interior 'partly filled with ovoid bodies of fine-grained calcite averaging 0.3 mm long and 0.12 mm wide, which we are inclined to accept as gametocysts. Similar bodies, generally of clear calcite are found scattered through the mud fillings and the matrix of other specimens. Of particular interest is a lens-shaped body of coarse calcite . . . within which are to be seen traces of five of the inferred gametocysts. This is interpreted as the remains of a complete gametangium'.

Elias (1947, p. 51) records one fragment of his *Permopora* 'as a fruiting stage, in all probability of *Permopora keenae* because it contains small subspherical or pyriform molds in the angles between the polygonal segments, suggestive of the occurrence of aplanosporangia in the club-shaped distal part of *Neomeris stipitata*'. The structures described are not clearly shown in his figures.

*Ischadites* (a Girvan example is dealt with below) is not considered a dasycladacean in the very thorough review of Rietschel (1969), and the structures interpreted as dasycladacean-reproductive by Kesling & Graham (1962, p. 950) are part of the outer calcareous plating seen in section.

In *Koninckopora* (Wood, 1943, p. 214) differences in calcification in the outer cells are explained as possible remains of former sporangia.

All these cases (except *Ischadites*) are possible remains of Palaeozoic choristospore development. None are really conclusive: all occur well before a fairly well-

documented record of Mesozoic choristospore evolution. Their evaluation is further discussed in Part 3 of this paper.

*Mastopora fava* (Salter) Stolley

Pl. 7, fig. 3; Pl. 8, fig. 4; Pl. 9.

DESCRIPTION. (a) *External* (abridged from Currie & Edwards). Probably spheroidal or ovoid in life, usually occurs in flat or convex fragments, sometimes as much as 5 cm in length and 4 cm in width, composed of rather shallow and sharp-edged hexagonal cups; in the centre of each cup is a small circular pore . . . The diameter of the cups ranges from 1.3 mm to 3 mm. *M. fava* was apparently calcified only in the region of the cups, hence from its large size easily collapsed.

(b) *Internal*. Traces of stem-cell and branches in one specimen were figured by Currie and Edwards (1943, pl. 11, fig. 3). No clear section comparable to that discussed for *N. parva* was, however, available to these authors, and my sections have shown only fragments and debris of the outer cups and long primary branches of full-grown plants. Amongst these sections, however, is one of outstanding interest, which I interpret as remains of a young *M. fava* of only 5.5 mm diameter (the adult diameter is eight times this or more). This specimen is from the Lower Llandovery, Mulloch Hill Group, Mulloch Hill, Girvan, Ayrshire, reg. no. V.26824.

The section is strawberry-shaped, representing the slightly crushed section of a presumed originally near-spherical thallus. The maximum diameter in section is 5.46 mm. A central reniform area is interpreted as a collapsed stem-cell. The larger zone surrounding is formed of close-packed radiating club-shaped branches, seen to divide terminally into three or probably four short club-shaped secondary branches. Due to crushing and random angle of section the plane of section cuts radially one side and tangentially the other. A typical primary branch is 1.3 mm in length, with the diameter at the slim (inner) end 0.078 mm, widening slowly to a near-terminal diameter of 0.208 mm. A typical secondary branch is 0.182 mm in length, with lesser (inner) diameter of 0.039–0.056 mm, widening outwards to a diameter of 0.056–0.078 mm.

There is another fragment showing similar structure, adjacent to the main thallus.

The interpretation of this fossil is best made by analogy with the development of the living *Bornetella*, which has a somewhat similar morphology to that of *Mastopora*, both having both club-shaped and spheroid species. In the development of the spheroidal *B. capitata* (Harvey) J. Agardh, as described by Valet (1968, p. 37, pl. 9 (6)), the normal early dasyclad development of thin erect stem-cell and appearance of successive spaced verticils of lateral side-branches is succeeded by a crowding and bunching together of new developing branches to form a near-spherical head of closely-packed green primary and secondary branches, without calcification: this is reached before a diameter of 0.5 mm is achieved. Subsequent growth consists of lengthening and proportional slimming of the branches from a proportionally short central stem-cell, development of the peripheral cortex from the expanded secondaries, and cortex-calcification, to give the adult hollow thallus of about 15 mm diameter.

The Silurian fossil described above is interpreted as the *M. fava* growth-stage corresponding to the early head of *B. capitata* at the pre-0.5 mm growth-stage. It is much larger, but *M. fava* is a much larger species than *B. capitata*. The branches of the Silurian species are nonverticillate, unlike *B. capitata*, but the two have much in common.

The factors influencing the preservation of such a soft crushable and perishable structure are not known to me. Presumably, very soon after burial in the sediment, before compaction, and with only slight crushing of the plant, the juicy plant tissue was replaced by calcium carbonate out of circulating solution, possibly by osmosis. Subsequent diagenesis has stained and in part replaced the calcite, and there has also been some pyritic replacement. This kind of preservation is very rare, but the present case is not in my experience unique, for the even more delicate *Lacrymorphus perplexus*, a supposed unicellular green alga, is preserved somewhat similarly in the Kurdistan Triassic (Elliott, 1958).

Within the Silurian fossil there are occasional crystals very similar to those seen in the Ordovician *M. parva*. Both are in my view due to post-fossilization diagenesis. If the interpretation of the Silurian alga as a young *M. fava* is correct, sporangia would not have been present at this growth-stage, and this supports the rejection of the views of Currie and Edwards on the 'reproductive bodies' in *M. parva*.

Order RECEPTACULITALES Rietschel 1969

Family RECEPTACULITACEAE Eichwald 1860

Genus *ISCHADITES* Murchison 1839

*Ischadites* sp.

Pl. 2, fig. 2; Pl. 10.

REMARKS. The Receptaculitaceae have long been problematic fossils, sometimes referred (amongst many other groups) to the Dasycladaceae (e.g. Kesling and Graham 1962). They have recently been reviewed in great detail by Rietschel (1969) who shows decisively their differences from Dasycladaceae, in spite of some similarities. He concludes, however, that they are green algae, and erects the order Receptaculitales for this wholly extinct group.

In this connection the living non-calcified *Dictyosphaeria* (Order Siphonocladales, Family Valoniaceae) is worthy of comparison. The thallus forms a hollow cushion of adpressed polygonal vesicles, and it eventually ruptures to form an irregular membrane. If such a plant grew more regularly (*Ischadites* is almost mathematical in the orientation of its plates, similar patterns occurring higher in the plant kingdom in some cacti) and if the alga calcified, so precluding normal rupture, then a similar structure to that seen in the fossil *Ischadites* might be preserved. This is not to postulate close relationship, for *Ischadites* has a characteristic and peculiar plate-pattern. There are however morphological resemblances and it does seem likely that it is an extinct green alga.

In the material examined a large thin-section shows a random section of an undoubted *Ischadites*, with characteristic plate-structure; this is from the Upper Ordovician of Balclatchie, Ayrshire, Mrs Robert Gray Collection, reg. no. V.15445a.

## Part III

THE EVOLUTION OF REPRODUCTIVE STRUCTURES OR ORGANS  
IN THE DASYCLADALES

INTRODUCTION. The dasycladacean flora described above from the Scottish Lower Palaeozoic is of interest in the relative primitiveness of the inferred position of the reproductive structures, in spite of the variety of form of thallus, especially that of the elaborate *Mastopora*. The supposed visible reproductive bodies of *M. fava* are shown to be inorganic. Presumably its true reproductive structures were non-calcified and located within the stem-cell, the "endospore" stage of Pia's terminology (Pia, 1920), as were those of the other simpler genera described.

PATTERNS OF DASYCLADACEAN REPRODUCTIVE STRUCTURE. In the Dasycladaceae the reproductive structures, as preserved in the fossils, yield little or no direct evidence of the sexual mechanisms involved, thus differing from the structures seen in fossil Melobesioids (Lemoine, 1961, 1971) or Chaetangiaceae (Elliott 1961). Conventionally known as sporangia, they are interpreted by analogy with what is known of living Dasycladaceae (cf. Valet 1969). Frequently resting cysts are formed which only germinate after breakup of the calcareous structure of the plant, whether before regeneration or after death, and many fossil genera must have been similar. The living *Dasycladus* itself is an exception to this, releasing gametes direct, as its calcification is confined to the exterior of the stem-cell. This is probably a secondary adaptation. The existence of *Chlorocladus*, a 'cysted *Dasycladus*' which has long been doubtful, has recently been confirmed by Valet (1969).

Pia regarded the primitive condition as that in which the sporangia were located within the thick central stem-cell; his endospore stage. For many genera this can only be inferred (though reasonably so) from the thick stem-cell and thin side-branches. Direct evidence of this condition occurs in the Triassic species *Diploporella phanerospongia* Pia and *D. tubispora* Ott, where calcified sporangia occur visibly within the stem-cell cavity, itself inside the elaborate calcified external branch-structure. Other apparently problematic fossils e.g. *Atractyloopsis* (Carboniferous and Permian) and *Aciculella* (Permian and Triassic), are interpreted as remains of dasycladaceans which calcified only their endospores or between them, so giving rise to cylindrical tubes or rods of hollow spheres, with no calcified trace of the branch-systems (Elliott, 1971a). Endospore genera are characteristic of the Palaeozoic and do not survive the Mesozoic so far as known. Endospory however has been observed as an abnormality in certain cultured living *Acetabularia* (Valet, 1968, 65-66).

A more advanced evolutionary stage of this sporangial migration within the plant is the cladospore, where the sporangia are located within thick swollen side-branches. This stage appears in the Permian (e.g. *Goniolinopsis*) is especially characteristic of the Mesozoic, and survives into the Palaeocene. In many genera the swollen primaries and diminished stem-cell diameter are taken as indirect evidence of cladospory. But there are more definite examples. *Triploporella* (Jurassic-

Cretaceous) shows swollen primaries filled with discrete sporangia, and the swollen spherical branches of *Cylindroporella* (Jurassic-Cretaceous) are obviously sporangial since they occur in verticils alternating with those of thin normal branches. The change from endospory to cladospory took place in different stocks at different times. In the Alpine Triassic *Diplopora annulata* Schäfhautl a dimorphism between presumed endospore and cladospore individuals is to be seen. The complicated explanations, both biological and taxonomic, of this by Pia (1920), have been simplified taxonomically by Herak (1957).

Another modification of the cladospore stage is the fusion of the swollen primary-branch verticils into calcified cups, as seen in *Clypeina* s.l. (Permian to Mid-Tertiary).

This genus has often been classified with the choristospore *Acetabularia* and *Acicularia*, showing similar terminal discs, usually single. But *Clypeina* appears before the choristospores, and is best interpreted as a modified cladospore (Elliott 1968, text-fig. 16).

In the third, last and most advanced stage of evolutionary sporangial migration within the plant, the choristospore stage, the sporangia are borne as separate structures upon the branch-system. This stage appears in the Mesozoic, is especially characteristic of the Tertiary and is seen in all living Dasycladaceae.

The position of the sporangia in living choristospores is variable as between different genera. In *Bornetella* they occur along the primary branches; in *Dasycladus*, *Cymopolia*, and *Neomeris* in the junctions of primary and secondary branches, in *Batophora* adjacent to the ends of both primary and secondary branches. In *Acetabularia* and *Acicularia* the reproductive structures are fused into terminal discs or cups, and a halfway stage to this survives in *Halicoryne*. Even more than the endospore-cladospore transition, the evolution from cladospore to choristospore took place in different stocks at different times in different ways. An early example of this may be seen in the Lower Jurassic *Eodasycladus ogilviae* (Cros and Lemoine 1966). Here, verticils show primary branches each dividing into secondaries, and they in turn into tertiaries. In some examples, one of the secondaries in each branch-system is swollen into a spherical sporangium, not giving rise to tertiaries but enveloped by the other dividing, secondaries. This is a specialization of cladospory which is transitional to a true choristospore.

A second, different transition is seen in the Upper Cretaceous *Cymopolia eochoristosporica* (Elliott 1968). Here swollen cladospore primary branches divide into a typical cymopoliform cluster of four thin secondaries with a small central spherical sporangium. The species shows in fact the evolutionary origin of the normal cymopoliform branch-structure seen in Tertiary and living species of the genus. It may be interpreted as partial transfer of the sporangial contents into a new independent organ, as opposed to conversion of an existing secondary branch into a sporangium. It follows that the existing choristospore patterns of sporangial distribution are probably of diverse origin.

The specialized reproductive discs of *Acetabularia* and *Acicularia* s. str. are derived from a structure such as that seen in *Halicoryne*; already choristospore, but with the gametangium larger than the sterile branch-system. Fusion of such gametangia led to the funnel or disc structure of *Acetabularia*.

REPRODUCTIVE ONTOGENY OF THE DASYCLADACEAE. Living dasycladaceans are a relict group, with several characters setting them apart from other green algae. *Acetabularia* especially has been studied under experimental conditions, and its normal and abnormal developments are known in some detail. It is especially remarkable in being, from one point of view, a giant unicellular alga. During most of the growth of the plant the large nucleus is located within the basal holdfast or rhizoid, but on completion of the terminal cap to maximum size the nucleus divides into numerous smaller nuclei, which travel up the stalk to the cap, where they form reproductive cysts for eventual release (Hämmerling 1931, 1934, 1953; Egerod 1952; Brachet 1965).

This pattern of reproduction is believed to be fundamental to the Dasycladaceae. Although eventual sexual mechanisms are not uniform (Valet 1969, p. 637) the large basal nucleus and its break-up and dispersal are believed to be characteristic of the family.

In the development of the thallus of living Dasycladaceae an early thin stem rising from the basal portion, develops successive whorls or verticils of simple side-branches. During growth these elaborate greatly, according to the generic pattern. *Dasycladus* itself shows elaborate but consistent repeated lateral branchings: in *Bornetella* the expanded terminations of the secondaries form the calcified cortex of the hollow spherical or club-shaped plant; in *Acetabularia* most of the branches are eventually shed and the final reproductive cap is borne at the end of a long naked stem. In all three the small nuclei derived from the break-up of the large basal nucleus pass up the stem-cell when they are technically endospores, through lateral branches when they are technically cladospores, and finally into distinctive separate reproductive structures (sporangia), peripheral or terminal in position, when they are choristospores characteristic of the species.

THE COMPONENT FACTORS OF DASYCLADACEAN EVOLUTION. With the above in mind, it is possible to suggest the separate basic factors which, in combination, have brought about the rich and varied pattern of dasycladacean genera ranging from Cambrian to Recent. These are three in number, two being fundamental and the third the reason for our knowledge, such as it is, of the fossil genera which very greatly outnumber living ones.

1. The first factor is a tendency to progressive elaboration of the thallus. With growth, increased complexity of branching develops for the plant's essential photosynthesis, and this is seen in both ontogeny and phylogeny. The early dasycladaceans were probably the result of evolution from a large unicellular chlorophyte. They show a thallus consisting of an irregular stem-cell, sometimes recumbent, branching or even anastomosing, and densely set with non-verticillate simple primary side-branches. The Cambrian Dasycladaceae are known to me from published accounts such as those of Korde (1957) and not from actual specimens, but they come in this category.

In the Ordovician-Silurian, such a pattern continues, but there are innovations. *Mastopora* and its allies show the first development of the large hollow thallus with calcified outer cortex, which reappears throughout geological time and is still present



in *Bornetella*. *Vermiporella* continues a primitive genus, but there is a tendency for evolution to the upright stem-cell so familiar in subsequent geological periods; e.g. the Ordovician *Intermurella* is an early example. Later in the Palaeozoic the transition to verticillate side-branches is made e.g. *Mizzia*, though the non-verticillate pattern survives into the Mesozoic e.g. *Macroporella* s. str. All subsequent Dasycladaceae are verticillate, to the present day.

*Mizzia* is also an example of the 'beaded thallus' pattern, more common in the Codiaceae, but seen in the living dasycladacean *Cymopolia*.

Early lateral branches are primitive and rather variable. In *Mastopora* they are already specialized. The 'diplopore' pattern of bunched branches so characteristic of the Triassic begins as early as the Devonian (Poncet 1966, 1967); this author suggests two lines of such evolution for the remainder of the Palaeozoic (one through *Velebitella* (Carboniferous) and then through a Permian diplopore) and so into the Triassic.

The 'fused reproductive disc' structure first appears in the Permian (Emberger 1958; Elliott 1968) and reappears in different guises to the present day.

Very many different patterns of branching, with primaries, secondaries, tertiaries and further branches, the branches in different proportions between different genera, mark the Mesozoic and Tertiary-Recent dasycladaceans.

The repetition of various structures in different genera at very different times has been stressed by Kochansky-Davidé and Gušić (1971).

2. The second factor is the migration of the small nuclei to peripheral positions in whatever vegetative-thallus structure has evolved. Endospore genera may be inferred from the proportionally large stem-cell of many primitive genera, and evidence is occasionally preserved calcified. A similar phenomenon is seen with cladospores (see above, pp. 368-369 for examples of these). Evidence of choristospores is very frequently preserved by direct calcification.

In reviewing *Broeckella* (Elliott 1962), a genus which shows cladospory as late as the Palaeocene, I wrote '. . . we do not clearly know the special advantage of choristosporic structures, whether a direct one in shedding elements more easily, or an indirect one in their being produced more freely and lavishly with no greater or even less strain on the metabolism of the plant, but although not properly understood it is a main trend in dasyclad evolution'.

Later, whilst still not able to answer this question, I was able to show that this major trend in dasyclad evolution, the shift of the reproductive bodies in position, had not saved them from marked decline and near-replacement by other, different, green algae in those environments suitable to both (Elliott 1968).

It can now be seen that the question I asked has no answer of the kind expected. The dasycladacean reproductive mechanism provides for peripheral dispersal of the small nuclei, and this occurs however elaborate the thallus, resulting in the fascinating range of structures detailed above. This has had no markedly beneficial effect in dasycladacean evolution, since it has not led to production of a more efficient mechanism, only to accommodation of the existing one. A comparable state of affairs is to be seen in the evolution of terebratellacean brachiopods (Elliott 1953),

where the development of very elaborate calcareous brachial structures as supports for the lophophore has not resulted, so far as can be evaluated, in an improved lophophore, nor helped in arresting the decline of the group.

3. The third factor is calcification. It is not known why some algae calcify and others not, since both, calcified and non-calcified, photosynthesize together under the same conditions side by side. This is a problem for a plant biologist trained in marine biochemistry and physiology. The Dasycladaceae calcify capriciously within the family, but consistently for each genus. With very heavy calcification, a record is preserved of all structures save the outer tips of fine branchlets. Lighter calcification can vary between a thin outer sheath which leaves no evidence of the plant within, or a thin stem-cell coating which bears no evidence of the branch-system without. The importance of this lies in the fact that except under very special circumstances, such as the immature *Mastopora* described above, calcification is usually the only direct evidence of marine algae to be preserved fossil. If a naked dasycladalean has been preserved, it may be the problematic *Inopinatella* of the Silurian (Elliott 1971b).

#### CONCLUSIONS

It can be seen that the varied and fascinating dasycladacean taxonomic variety is the resultant of their reproductive nucleus-dispersal operating in the enlargement and elaboration of the vegetative thallus, the results preserved mostly, in part, or very little by the amount of calcification peculiar to the particular genus involved.

With this in mind, the question of the alleged Palaeozoic choristospores can be reviewed. Granted that the evidence as preserved is doubtful, and that they occur before the main cladospore-choristospore trends; are they possible?

That dasycladaceans repeated the same evolutionary trends in different families is undeniable. The tiny Bereselleae of the Carboniferous, with their own evolution of annularly-grouped zones of simple thin side-branches, yet evolved one genus (*Exvotarissella*) showing the same phenomenon of secondarily dividing thickened primary branches, familiar in the main course of dasyclad evolution (Elliott, 1970b).

Clearly it is possible that precocious reproductive structures (from an evolutionary point of view) could have developed. We see now that they would not have had much if any advantage. They must therefore be judged by the evidence, and this unfortunately is doubtful. *Mastopora parva* certainly is not choristospore; the others quoted are not indubitably convincing from the evidence as presented.

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## NOTE

Due to circumstances connected with delayed publication, the important memoir of Dr. M. H. Nitecki on North American Cyclocrinitid Algae (Fieldiana Geology, vol. 21; 1970), in which *Mastopora* is merged in synonymy with *Cyclocrinites*, is not discussed in this paper.

## EXPLANATION OF TEXT-FIGURE

Diagrammatic representation of selected evolutionary stages in Dasycladacean reproductive evolution. Each figure shows a portion of the stem-cell on the left, and the appropriate branch-structure on the right. Solid black = calcification; light spaced stipple = vegetative tissue; heavy close stipple = reproductive bodies (separate small calcified sporangial bodies of fig. 4 not shown stippled).

- FIG. 1. *Diplopora tubispora* Ott, Triassic. Endospore reproductive bodies with calcified walls; diplopore lateral branches in outer calcification.
- FIGS 2, 3. *Diplopora annulata annulata* (Pia) Herak, with presumed endospore bodies, and *D. annulata dolomitica* (Pia) Herak, with presumed cladospore reproduction. Triassic; a possible example of endospore-cladospore change within the single species.
- FIG. 4. *Triploporella* sp., Jurassic-Cretaceous. Cladospore structure; primary branches crowded with sporangial bodies.
- FIG. 5. *Eodasycladus ogilviae* Cros and Lemoine, Jurassic. Adaption of one secondary branch (from several to each primary) to take reproductive bodies. This is one possible cladospore-choristospore transition.
- FIG. 6. *Cymopolia eochoristosporica* Elliott, Cretaceous. Development of a small cymopoliform branch-structure of long sterile branches and central sporangium upon a large cladospore primary branch, with partial transfer of the sporangial contents. This is a second possible cladospore-choristospore transition.
- FIG. 7. *Batophora oerstedii* J. Agardh, Recent. A living non-calcified choristospore dasycladacean, with reproductive bodies grouped at the junctions of primary, secondary and tertiary branches.

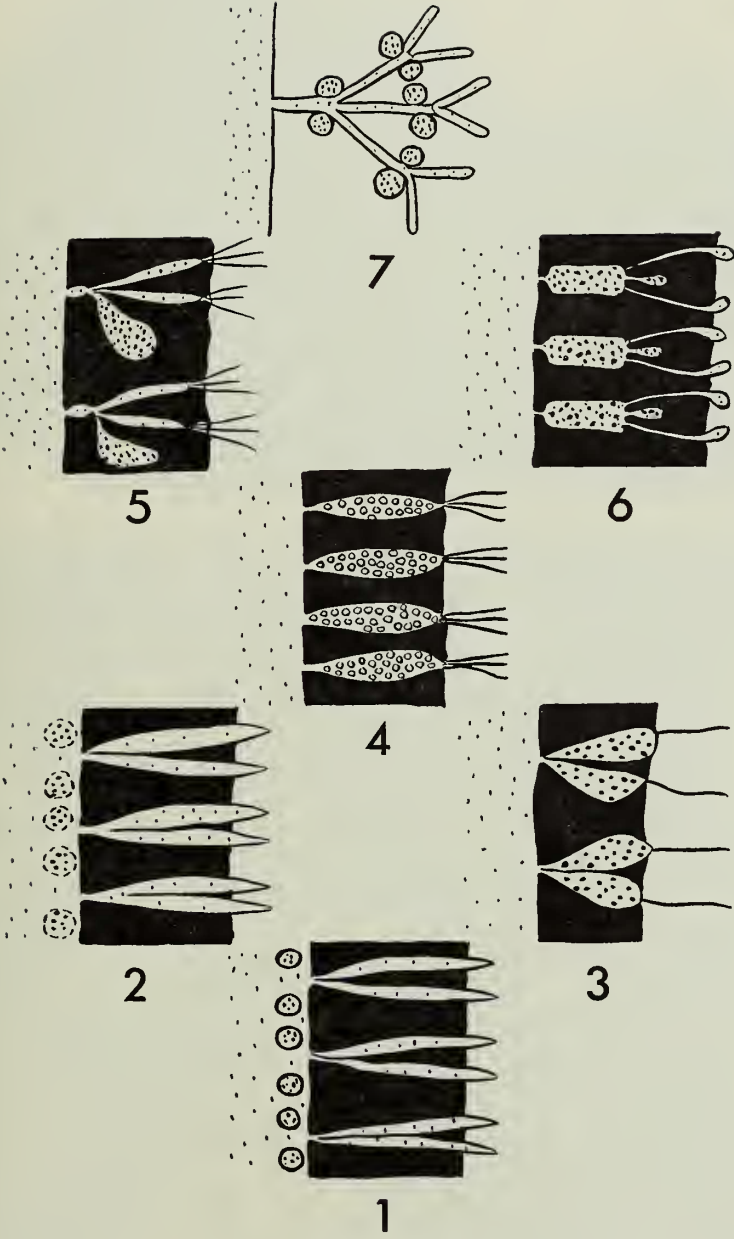


PLATE 1

FIGS 1, 2. *Dimorphosiphon rectangularis* Høeg. Middle Ordovician: Helgoen, Lake Mjøsen, Norway. 1. Longitudinal section,  $\times 9$ ; V.23778. 2. Transverse sections,  $\times 14$ ; V.42601.





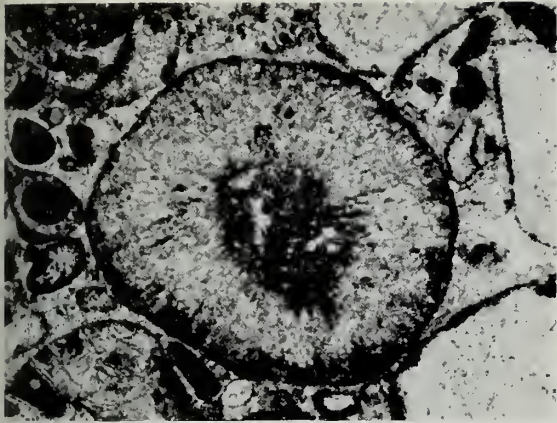
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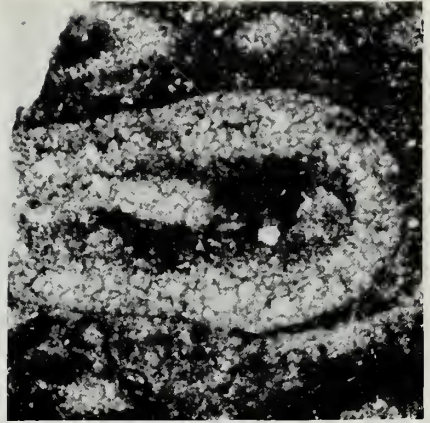
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PLATE 2

- FIGS 1, 2. *Dasyoporella* cf. *norvegica* Hoeg. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire, Scotland. 1. Transverse section,  $\times 27$ ; V. 17067. 2. Longitudinal section,  $\times 34$ ; V.55325a.
- FIG. 3. *Ischadites* sp. Oblique section of meromes (skeletal elements) in position,  $\times 14$ . Upper Ordovician, Lower Ardmillan Series, Balclatchie Group (Caradocian); Balclatchie, Girvan, Ayrshire, V.15445a.
- FIGS 4, 5. *Dimorphosiphon rectangularis* Hoeg. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire, V.55325a. 4. Oblique-transverse section,  $\times 14$ . 5. Oblique longitudinal section,  $\times 14$ .



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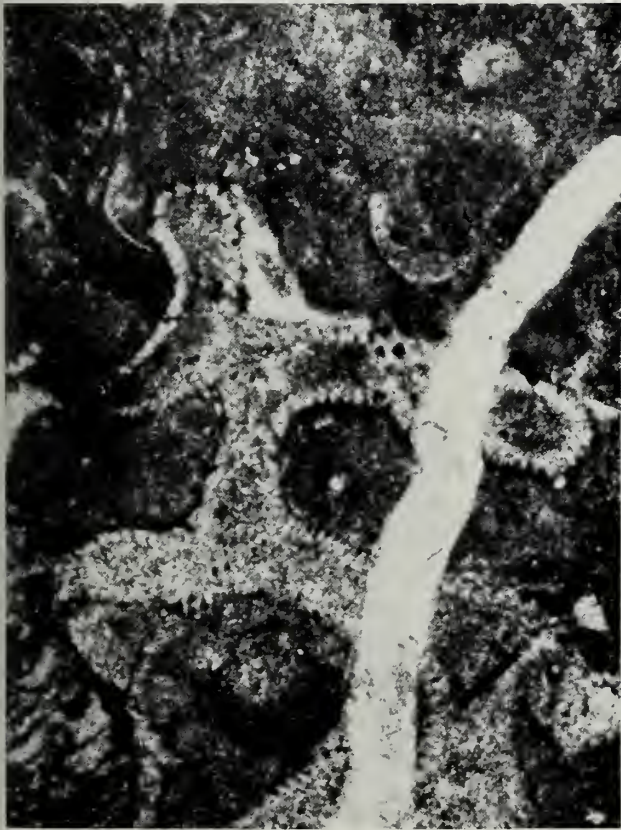
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PLATE 3

- FIGS 1, 2. *Vermiporella eisenacki* sp. nov. Middle Ordovician, Stinchar Limestone; Tramitchell Quarry, Girvan, Ayrshire, V.54162b. 1. Paratype, random sections,  $\times 21$ . 2. Holotype, section of branching twisted thallus,  $\times 27$ .
- FIG. 3. *Intermurella scotica* gen. et. sp. nov. Longitudinal section,  $\times 17$ . Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire, V.55302a.



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PLATE 4

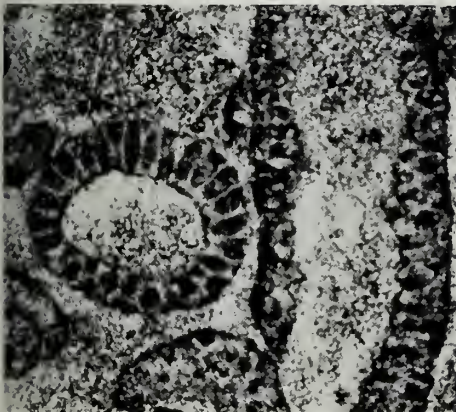
FIGS 1-4. *Intermurella scotica* gen. et. sp. nov. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire. 1. Holotype, longitudinal section,  $\times 14$ ; V.55302a. 2. Paratype, oblique section of curved individual,  $\times 17$ ; V.55302c. 3. Paratype, transverse section,  $\times 22$ ; V.55302b. 4. Oblique-transverse section,  $\times 23$ ; V.55302c.



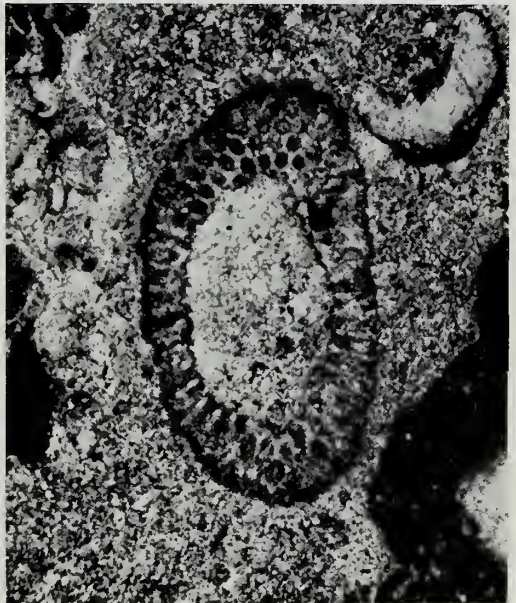
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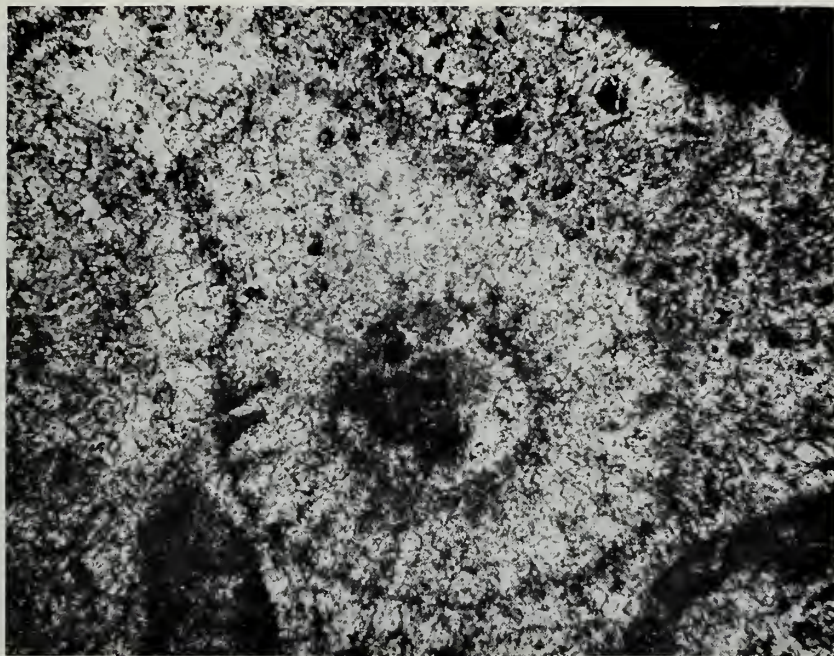


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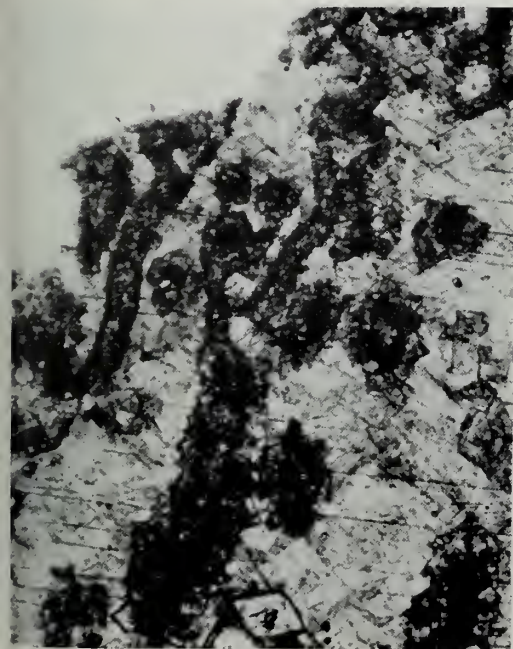
PLATE 5

- FIG. 1. *Vermiporella* cf. *borealis* Hoeg. Upper Ordovician, Craighead Limestone (Caradocian); Craighead, Girvan, Ayrshire. Random Section,  $\times 86$ ; V.55302b.
- FIG. 2. *Mastopora parva* (Nicholson and Etheridge) Pia. Upper Ordovician, Balclatchie Group (Lower Caradocian); Balclatchie, Girvan, Ayrshire. Radial primary branches interpreted as dividing into secondaries, somewhat displaced,  $\times 45$ ; V.16123a.
- FIG. 3. *Vermiporella* sp. Random section, near-longitudinal,  $\times 35$ . Upper Ordovician, Stinchar Limestone (Caradocian); Benan Burn, Barr, Ayrshire, V.54386a.





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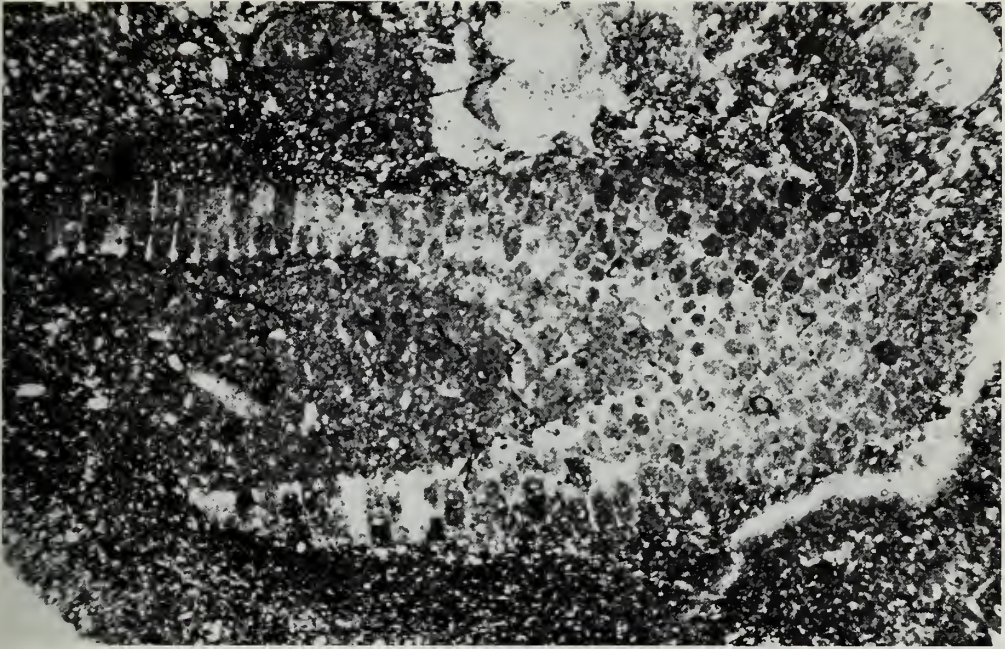
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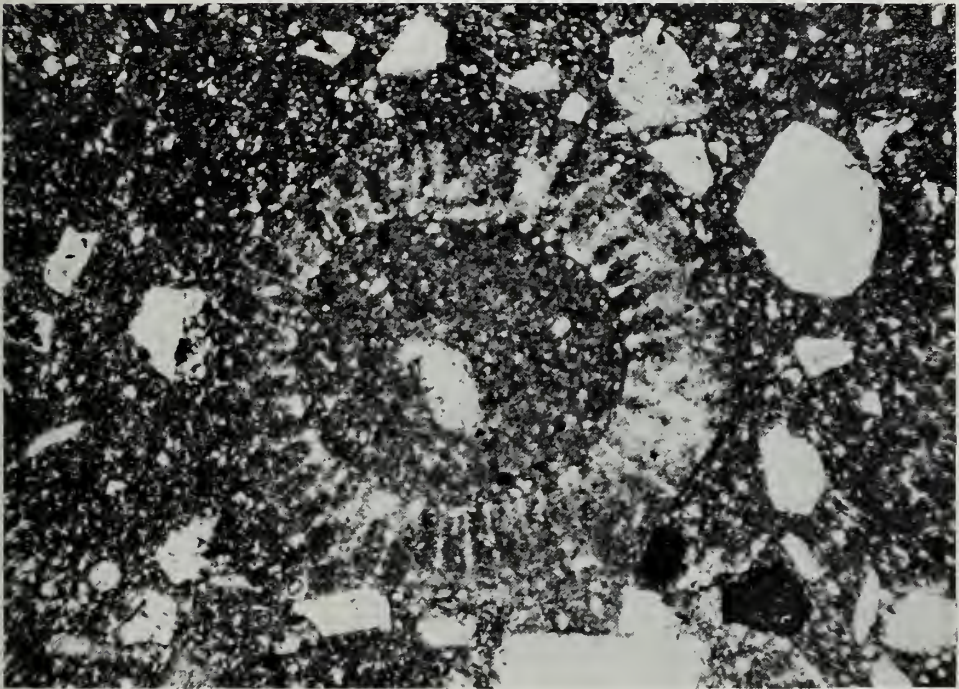
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PLATE 6

FIGS 1, 2. *Novantiella ordoviciana* gen. et. sp. nov. Upper Ordovician, Lower Ardmillan Series, Balclatchie Group (Caradocian); Balclatchie, Girvan, Ayrshire. 1. Holotype, oblique-longitudinal section,  $\times 24$ ; V.16124a. 2. Paratype, transverse section,  $\times 30$ ; V16124b.



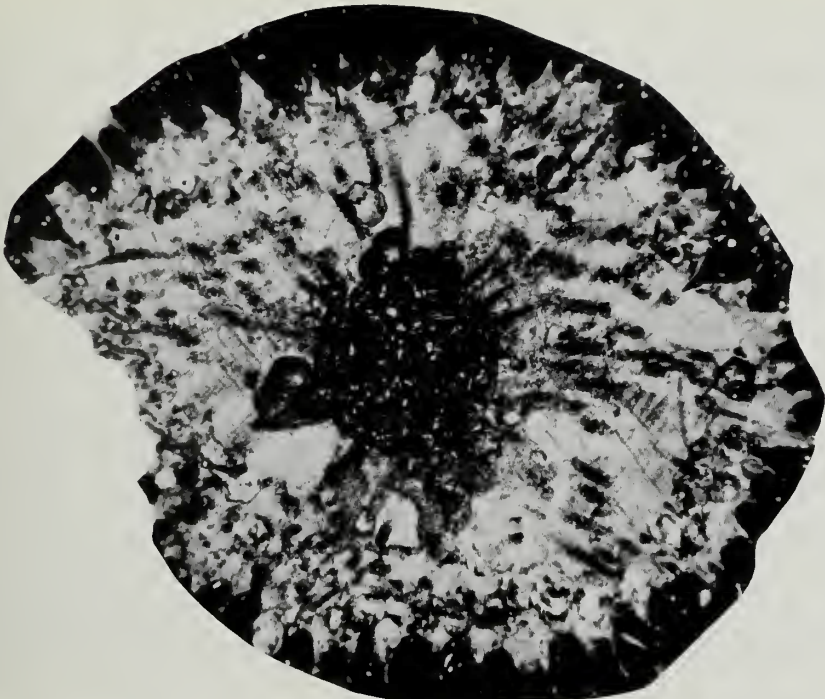
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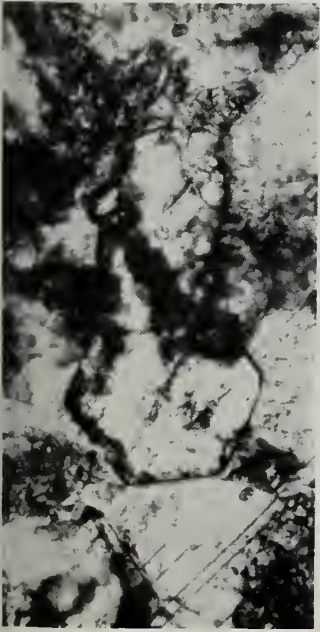
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PLATE 7

- FIG. 1. *Mastopora parva* (Nicholson and Etheridge) Pia. Upper Ordovician, Balclatchie Group (Lower Caradocian); Balclatchie, Girvan, Ayrshire. The unique transverse section described by Currie and Edwards (1943),  $\times 10$ ; V.16123a.
- FIG. 2. Detail of a crystal from the interior of the *M. parva* in fig. 1;  $\times 45$ .
- FIG. 3. *Mastopora fava* (Salter) Stolley. Lower Silurian, Mulloch Hill Group (Lower Llandovery); Mulloch Hill, Girvan, Ayrshire. Uncrushed, solid, young specimen,  $\times 4.5$ ; V.16110.



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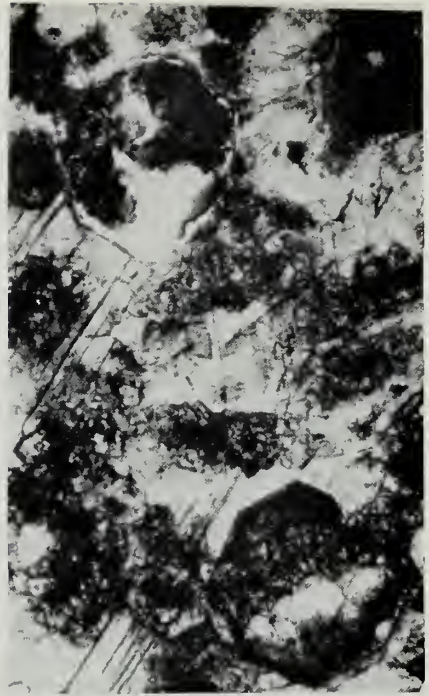
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PLATE 8

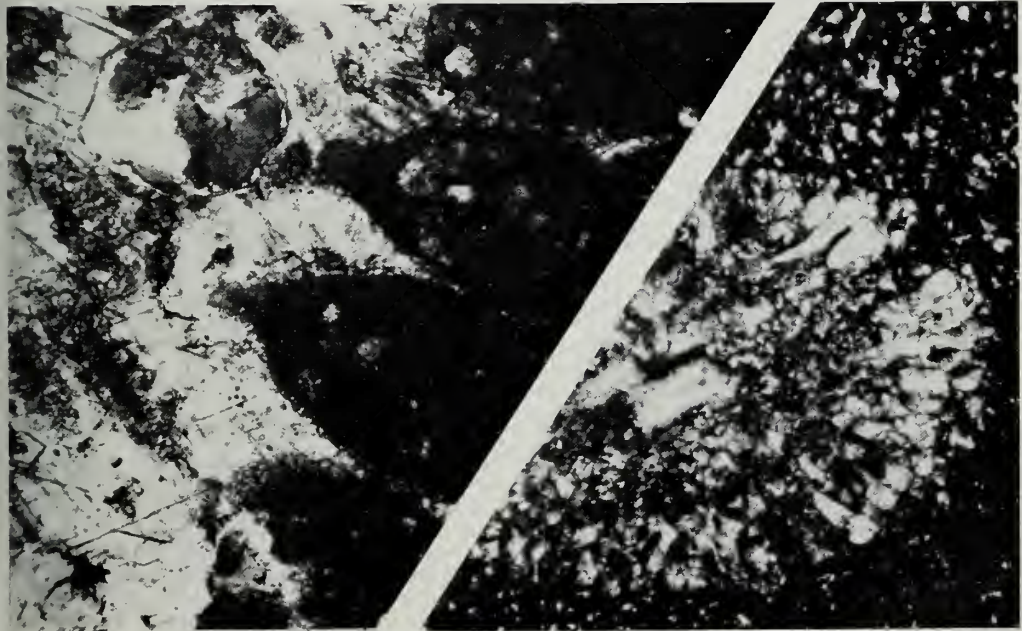
- FIGS 1-3. Detail from section of *Mastopora parva* (Nicholson and Etheridge) Pia (seen Pl. 7, fig. 1) Upper Ordovician, Balclatchie Group (Lower Caradocian); Balclatchie, Girvan, Ayrshire, V.16123a. 1. Primary branches radiating from central stem-cell,  $\times 45$ . 2. Crystals previously interpreted as reproductive bodies,  $\times 44$ . 3. Matrix-filled cups of the outer, calcified layer, and one crystal,  $\times 45$ .
- FIG. 4. Immature *Mastopora java* (Salter) Stolley. Lower Silurian, Mulloch Hill Group, (Lower Llandovery); Mulloch Hill, Girvan, Ayrshire. Random section of moderately crushed individual showing distorted central stem-cell (originally near-circular) and adpressed, radial, uncalcified primary and secondary branches,  $\times 14$ ; V.26824b.



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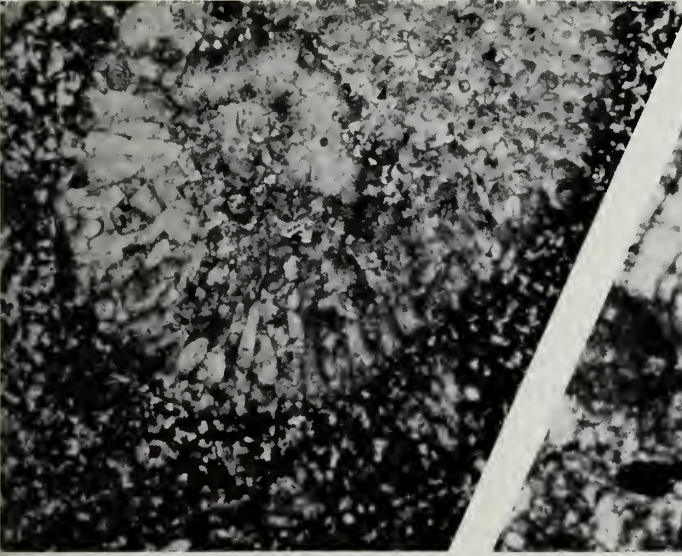
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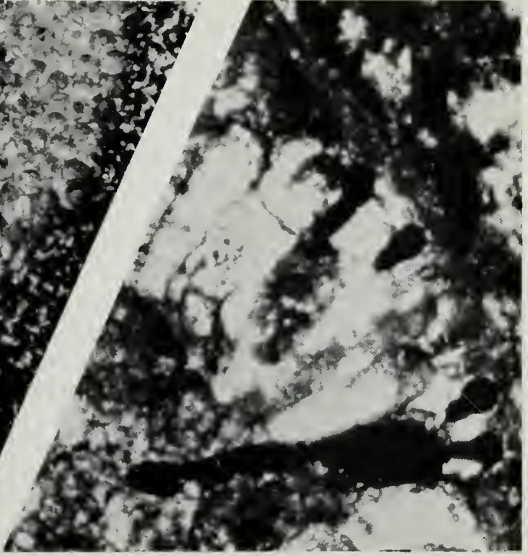
PLATE 9

- FIGS 1-3. Immature *Mastopora fava* (Salter) Stolley. Lower Silurian, Mulloch Hill Group, (Lower Llandoverry); Mulloch Hill, Girvan, Ayrshire. 1. Random section of moderately crushed individual showing distorted central stem-cell (originally near-circular) and adpressed radial, uncalcified primary and secondary branches,  $\times 14$ . A different thin-section to that shown in pl. 8, fig. 4, V.26824a. 2. Detail of primary and secondary branch systems, filled with white calcite and black pyrites, from a detached fragment of the same or possibly another individual in thin-section, V.26824b;  $\times 68$ . 3. Detail of primary and secondary branches, mostly calcite-filled but a little pyrites, from specimen in fig. 1 above,  $\times 68$ ; V.26824a.

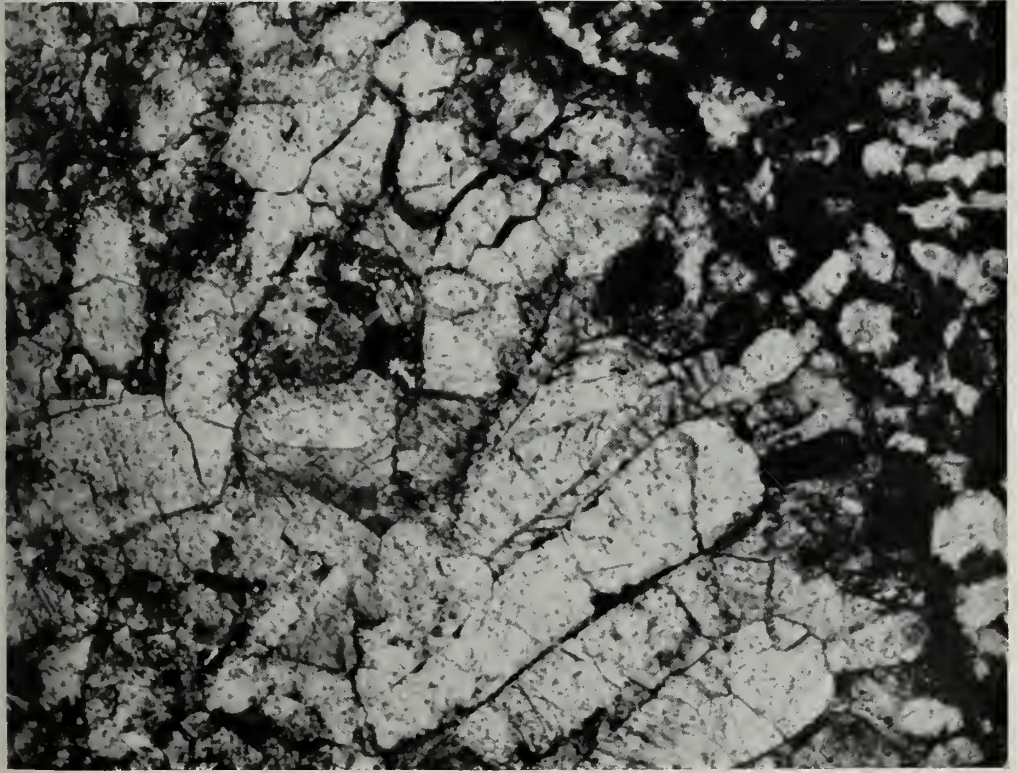




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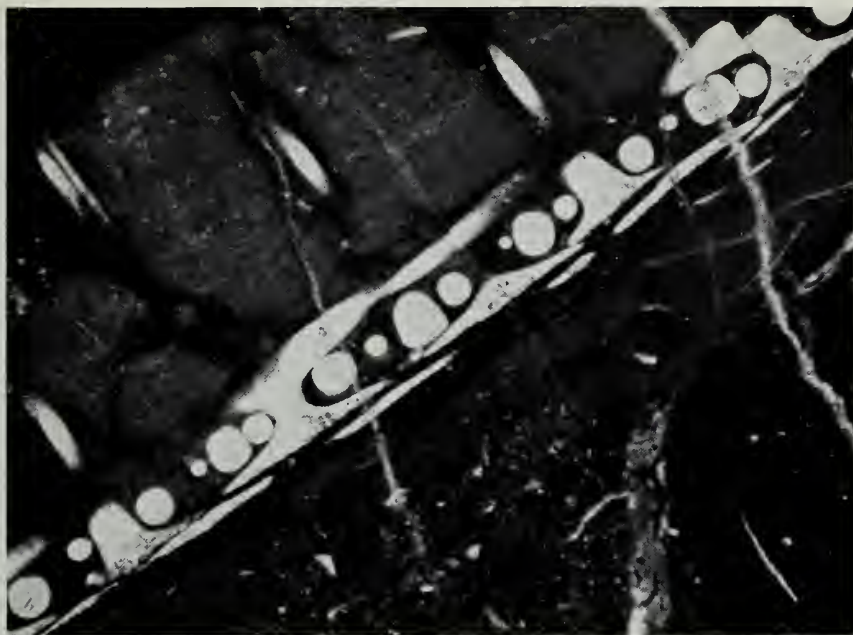
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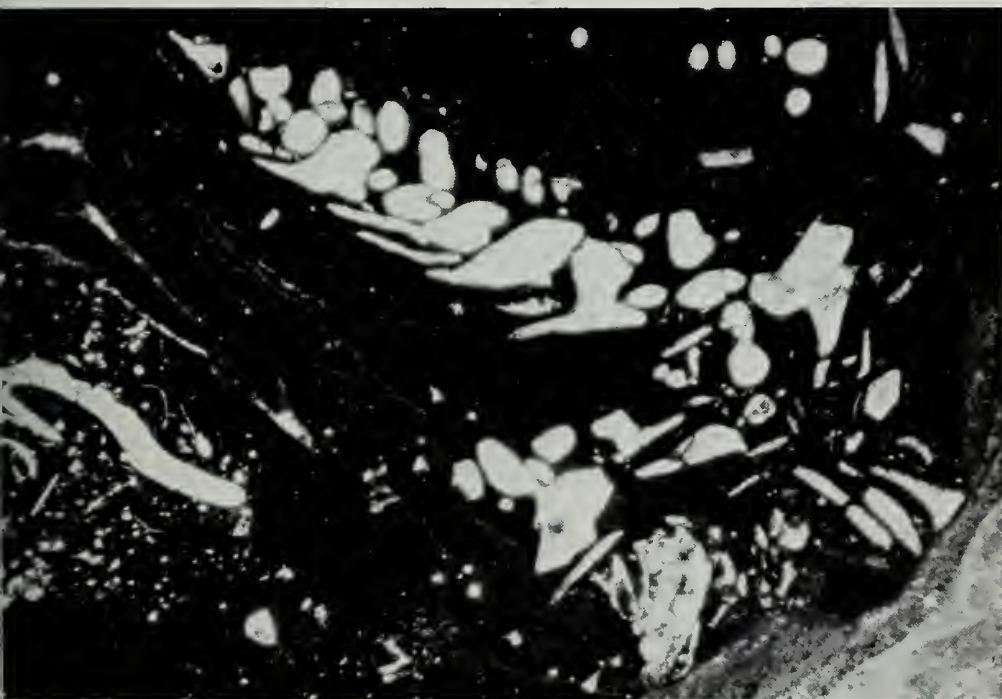
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PLATE 10

FIGS 1, 2. *Ischadites* sp. Upper Ordovician, Lower Ardmillan Series, Balclatchie Group (Caradocian); Balclatchie, Girvan, Ayrshire, V.15445a. 1. Vertical section of outer 'wall' or plating, showing the overlap structure of the merome outer plate and arms, sometimes misinterpreted as dasycladacean reproductive bodies; radially-set tangential cuts of the inner merome 'pillars' below,  $\times 17$ . 2. Random section of displaced skeletal elements,  $\times 14$ .



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